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LARVAL STADIA

OF THE WESTERN PINE BEETLE

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INTRODUCTION

In common with most other species of barkbeetles, characteristics of the larval stadia of the western pine beetle (Dendroctonus brevicomis Lec.) have not been determined. However, recent investigative work involving the effects of temperature, both as a lethal factor and as a factor in development, has made it necessary to determine the stadia represented in the experimental material.

CRITERIA OF DEVELOPMENT

Various means have been used in measuring the changes involved in the successful development of insects. Increase in weight or in size may be used but, as individuals of D. brevicomis vary greatly in both weight and size, the use of either method of determining the instar to which any given individual belongs is impracticable.

Rearing of individuals through the successive stadia and observation of the ecdyses is a direct method. However, in the species concerned, the entire portion of the larval life is spent in phloem or outer bark in which the individuals are hidden from view. In addition, although it may be possible, successful rearing of larvae in natural food material, but under laboratory conditions allowing observance of the development of individuals, has not yet been accomplished. Unsuccessful development, unhealthy brood or abnormal prolongation of the growth period often develops, even when blocks are removed from an infested tree or when such a tree is felled.

In some insect species it is possible to discover and count the number of larval skins cast by an individual during its development. However, the western pine beetle is extremely small in the younger stadia, follows a tortuous path in formation of its larval gallery and utilizes a food material of such a character as to make the use of that method difficult and productive of extremely uncertain results.

Measurement of the head capsule or of some of its parts was first used in determining the number of instars in Lepidoptera by Dyar (1890). Since that time application of the rule derived from that study has been extended to species of other orders by many students of the subject. The hypothesis, on which this rule is based is that, for each insect species, there is a definite factor which, if mean measurements of the first, last and one adjacent instar are known, will fairly accurately determine the mean measurements of intervening instars. In recent years the incomplete applicability of that hypothesis has been shown, not only for some species having a prepupal stage (Taylor, 1931) but also for some in which observed ecdyses did not agree with the number calculated by use of the rule (Peterson and Haeussler, 1928).

Often this divergence appeared to be the result of differences in the development of the sexes (Miles, 1932). According to Uvarov (1928, p-313) and Chapman (1925, p-141), it has been shown that modification of nutritional factors may result in an unusual number of ecdyses.

Another method, utilizing measurements of the head capsule, consists of periodic sampling of a given population and measurement of all individuals in the sample (Taylor, 1931, and Metcalfe, 1933). It has been found that measurements of individuals of a given instar tend to have a normal distribution about a mean and that the means of each instar will occur as peaks in the distribution curve. However, it is obvious that, should divergence between the actual and apparent total number of instars appear, either due to an instar such as the prepupal, in which no enlargement of the head capsule may occur, or due to differences in the sexes, such differences would not be revealed by the sample method.

MEASUREMENTS OF WESTERN PINE BEETLE LARVAE

Head capsule measurements were resorted to in determining instars of the western pine beetle larvae, other methods having been considered nearly impossible, difficult or unsatisfactory. The width of the capsule was selected as that measurement has been found in many other studies to be as satisfactory as measurement of the length of the head or width of the frons.

DYAR'S METHOD.- Dyar's rule has been applied successfully to a nearly related species, the douglas fir beetle (Bedard 1933). Bedard described the use of an artificial means of securing first and second instar larvae. However, it was doubted if that method would be successful in dealing with the younger stages of the western pine beetle. Accordingly tests were made.

65 eggs were placed in pieces of green phloem which were firmly secured between two glass plates. Of that number 58 eggs hatched. On removal of the larvae, after observation for from 12 to 20 days without indication of ecdysis, but 7 larvae remained alive. Measurement of the head capsule widths of these larvae showed all but one lay within the range of the first instar. Six of the seven measurements were greater than the mean of the first instar as determined by the sample method, the results of which will be described later. It was apparent as the experiment progressed, that the larvae did not react normally, were unhealthy and, if nutrition affects the head capsule size, probably would not have given measurements applicable to a normal and healthy population. Examination of the larval mines failed to reveal any trace of cast skins, but it is believed possible that ecdysis occurred and that unsatisfactory nutritional conditions produced second stadium larvae, only one of which had a sufficiently large head width measurement to place it in its proper position in a normal population.

As a check on these results, and to determine if the elapsed period of time had been sufficient to allow ecdysis, larvae were collected from the same block from which the eggs were secured for the artificial rearing. Measurement of head widths of 20 larvae showed 7 were first instar larvae, 10 second instar and 3 belonged in the third instar group, as established by the population sample method. It is significant that measurements centered near the means of the instar represented in this population. It is evident that Bedard's method is not satisfactory for use in rearing the western pine beetle, not only because of a high mortality but also because of an evident retardation and abnormality of development.

POPULATION SAMPLE METHOD.- In the course of brood studies in the Modoc National Forest during the 1934 season, periodic collections were made from several trees during the entire period of development of the first seasonal generation. This material, as cut from the bark, was immersed in hot water and preserved in 50% alcohol. No apparent distortion of soft tissues occurred and it is unlikely distortion of chitinized portions were caused by the method of preparation. This material, numbering over 1200 individuals, was measured as a sample of the population. A distribution curve (Fig. 2), drawn from the results of the measurements, showed four major peaks. Each peak, with the exception of that representing the fourth instar, indicated a nearly normal distribution around a mean. Intermediate forms were found and there does not appear to be any sharp division between the instars. It is probable there is some overlapping, but its extent can be proven only by actual observance of a number of ecdyses of individuals having measurements in the intermediate zones.

Theoretically this overlapping raises considerable question as to the maximum variation of head widths in each stadium. Practically, however, and in determining the instar of experimental material, the intermediate measurements are of little importance. Intermediate measurements constitute only 2% of the total, if we consider the single central intermediate measurement between the peaks as worthy of exclusion, but 7% if it is believed necessary to exclude the three intermediate classes occurring between each peak curve.

FOURTH INSTAR LARVAE.- The curve representing the fourth instar does not appear to be a normal distribution curve, but does not represent two instars. The fourth instar includes individuals of active and feeding larval form and of an inactive prepupal form. However, no ecdysis occurs to distinguish these two forms as separate instars. It is probable that the lack of a normal distribution curve in the fourth instar is due chiefly to the accumulation of growth deficiencies in individuals that have developed under less favorable conditions. It is known that infested outer bark often contains numbers of small-sized individuals which, as a group, appear to be more numerous in those trees in which easily discernible unfavorable nutritional conditions have occurred.

In order to test this 100 small larvae, taken from the bark layers usually supporting fourth instar brood and a sample of which pupated without ecdysis, were examined. Head width measurements showed the range to be from .8036 mm to .9996 mm, with a mean of .9039 mm. This is .0701 mm less than the mean of a normal population, yet the distribution curve of the 100 specimens taken at random from a larger lot is normal. It is believed support is given by the above figures to the theory that growth inhibiting factors during development cause the smaller-sized but full-grown individuals. Further support is given by results of measurements of brood reared under noticeably unfavorable conditions of nutrition in artificially infested blocks. 39 larvae taken from such a block infested by late first seasonal generation individuals of the Modoc area, which, under field conditions, had completely emerged from infested trees by fall, showed a fairly normal distribution curve for the fourth instar when measurements were made at Berkeley in November. A minimum of .7644 mm. and a maximum of .9996 mm was found, the mean being .8822. The mean of this population is intermediate between the third and fourth instar means of a normal field population, yet there is no indication in the distribution curve that two instars are represented. Some pupation and a slight amount of emergence had occurred in the infested block.

MEAN MEASUREMENTS.- For practical purposes, the means of the four instars, as determined from the collections of a normal population sample developing under field conditions, are as follows: The minimum and maximum measurements were determined arbitrarily as the minimum points between the successive peaks of the distribution curve of the population sample.

Instar	No. Individuals	Mean	Standard	Minimum	Maximum
1	79	.4179 mm	± .0258	.3528 mm	.4704 mm
2	235	.5924 mm	± .0370	.4900 mm	.6664 mm
3	390	.7745 mm	± .0411	.6860 mm	.8624 mm
4	538	.9740 mm	± .0453	.8820 mm	1.0976 mm

The differences between the means of successive instars show no constant factor. The factor between the first and second instar is .7054; that between the next two instars is .7648 and that between the third and fourth is .7957.

It is apparent that, although the population sample method gives definite evidence of four instars, the means of each instar, as determined from the distribution curve, do not have the constant relationship postulated by Dyar's rule. However, the divergence is not excessive and may be partially accounted for by the possible overlapping of the instars. It is probable that growth inhibiting environmental conditions, which appear to have extreme effects under artificial rearing conditions and noticeable effects in some trees under field conditions, may also be responsible for some of the divergence.

RELATIONSHIP BETWEEN STADIA AND LARVAL HABITS

Figure 1 shows a series of average sized specimens and illustrates the comparative size of the egg, four larval instars, pupa and callow adult.

In general, the life history of the insect is as follows: Eggs are laid by the attacking parent adults in niches cut into the phloem along the sides of galleries constructed by the adults. On hatching the small larvae feed for a period in the phloem, forming minute galleries in that substance and progressing toward the covering of dead outer bark that encircles the phloem layer on the tree. Migration into the dead outer bark, which is accompanied by a marked change in food materials, soon occurs and subsequent larval development continues in the relatively short mines in the outer bark. After a period of feeding, each larval constructs a small cell, becomes quiescent and assumes a prepupa condition. Pupation occurs in the cell, as does the change to the adult stage. Some time is required before the adults darken, after which they bore their way to the outer surface of the bark layer and emerge.

It was desired to determine which stadia occurred in the phloem and which in the outer bark. Accordingly larvae were secured from brood in which some individuals were in the phloem and others just within the outer bark layers. Individuals taken from the phloem were separated from those taken from the bark. It was found that, of the 84 larvae secured from the phloem, 45.2% were first instar and 54.8% were second instar larvae. 53 individuals from the bark showed no individuals in the first instar, 81.1% were in the second instar and 18.9% were in the third instar. From this it is apparent that the larvae undergo one ecdysis in the phloem, then migrate and undergo the second and third ecdysis in the outer bark. Studies of time in relation to development appear to show the first and second stadia require approximately equal periods under similar conditions. The third stadium requires but about half as long as either of the two preceding stadia and the fourth instar, which includes the inactive prepupal form, requires approximately twice the period necessary to complete either of the first two instars.

CONCLUSIONS

In selecting material for experimentation, it appears that, almost regardless of size, brood from all except the inner portions of the outer bark will be fourth instar individuals. Size of these larvae, instead of indicating stage of development or age, apparently is largely the result of environmental, probably nutritional factors that have affected the individual during development. Material from the bark layers within a short distance of the phloem is either in the second or third instar. However, the short duration of the third instar apparently would make collections from this area chiefly second instar larvae. First instar material can be collected in the phloem soon after the eggs hatch and before long mines have been developed. Second instar material may be obtained in the outer phloem, as well as in the inner bark layers.

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FIGURE I

No. 9203

Examples of average individuals (approximately natural size) of the various stages of the western pine beetle (Dendroctonus brevicomis Lec.). The egg, which is at the extreme left in the picture and can scarcely be seen, is followed by individuals of the 1st, 2nd, 3rd and 4th larval stadia. The 4th instar larva is the active type, as evidenced by the curved body. The prepupal type is no larger but is of a yellowish color and the body is straight. The great increase in body size that takes place in the 4th instar is shown by the photograph. The pupal stage is to the right of the 4th instar larva and an average sized adult is at the extreme right of the series.

Photo by J.E.Patterson

HEAD WIDTHS OF WESTERN PINE BEETLE LARVAE

DISTRIBUTION CURVE